



## Evolutionary trends and stasis in carnassial teeth of European Pleistocene wolf *Canis lupus* (Mammalia, Canidae)



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### ABSTRACT

The evolutionary trends of tooth size in quaternary carnivores support an almost direct association with climate. However, phenotypic trait may follow distinct tempo and mode of evolution such as Brownian, Ornstein–Uhlenbeck or random walk. Here, we investigated the morphometric variations and evolutionary trends in the carnassial teeth size of the European wolf (*Canis lupus*) by means of modern statistical tools. Recent contributions highlighted linear increase trend in tooth size through the Pleistocene, but those differences in time have not been tested using modern statistical strategies. Examining a wide sample of linear measurements of carnassials of extinct and extant wolves (486 M<sub>1</sub> and 491 P<sup>4</sup>), we tested which evolutionary model (random walk, stasis, Ornstein–Uhlenbeck) better explains the dimensional pattern of teeth through time at the continental scale and at the regional scale (France and Italy). Our results clearly show different models for the carnassials of *C. lupus*. Lower and upper carnassials for the entire sample of *C. lupus* are characterized by a directional trend, whereas Italian and French subsets show a random fluctuation of carnassials size through time. The carnassials dimensions are not directly correlated with the climate changes during the Middle–Late Pleistocene and Holocene, but they are possibly correlated with spread of the cold mega-fauna in Europe, and thus with the changes in the dietary regime.

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### 1. Introduction

Morphometric variations and evolutionary trends through time in Pleistocene species have been investigated in recent years by several authors using different statistical strategies (Lacombat, 2009; Piras et al., 2009, 2012; Magniez, 2010; Desantis et al., 2011; Nishioka et al., 2011; Pandolfi et al., 2011; Raymond and Prothero, 2011; Stefaniak et al., 2012; Lozano-Fernandez et al., 2013; Mazza and Bertini, 2013; Meachen et al., 2014; O’Keefe et al., 2014; van der Made et al., 2014). Several works focused on sequences of fossil populations in order to investigate phenotypic changes and their causes during a time span, the Pleistocene, characterized by important climatic changes (Pandolfi et al., 2011; Mazza and Bertini, 2013; van der Made et al., 2014). Several contributions revealed stasis in time series-oriented paleontological

studies (cfr. Piras et al., 2009). Since 1972, palaeontologists investigated on the importance of stasis during evolution (Eldredge and Gould, 1972). Stasis is a central point inside the Punctuated Equilibria Theory (Eldredge and Gould, 1972; Gould and Eldredge, 1977; Gould, 2002; Eldredge et al., 2005). The major focus of this evolutionary model is that the phenotypes are stable through time and no directional trends are observable. The causes of the stasis could be: a) absence of variability; b) balancing selection; c) developmental constriction; d) habitat tracking; e) population structure: a species being structured in semi-isolated metapopulations. Different isolated populations experience different selective pressure thus returning a no neat phenotypic change in time (Wright, 1932; Eldredge and Gould, 1972; Gould and Eldredge, 1977; Gould, 2002; Eldredge et al., 2005).

Most paleontological studies set apart between patterns of stasis, random walk, and directional evolution. Stasis *sensu stricto* can be defined as when the variance of the total time series sample is not significantly larger than that of a single population in a time lapse (Wood et al., 2007; Piras et al., 2009, 2012). The random walk

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could be considered as a stasis *sensu lato*, defined as no neat change in successive steps of population mean values across a discrete ordered time sequence (Hunt and Carrano, 2010). Directional evolution is characterized by a significant trend in population means during the considered time intervals (Wood et al., 2007; Piras et al., 2009, 2012). A particular case of directional evolution for an evolutionary process with selection or drift is the Ornstein–Uhlenbeck model (Hansen, 1997; Butler and King, 2004; Piras et al., 2012), which represents a random walk with a general tendency to an adaptive optimum.

Morphometric variations in the wolf (*Canis lupus*) have been investigated by several authors but without testing for any evolutionary trend (Boudadi-Maligne, 2010, 2012; Brugal and Boudadi-Maligne, 2011; Flower, 2012; Flower and Schreve, 2014; van der Made et al., 2014). The oldest fossil record of the modern wolf is reported in the Olyor fauna (Siberia) and in the Cripple Creek Sump (Alaska) during the Middle Pleistocene. Several authors have proposed an origin of *C. lupus* in Beringia (Sher, 1986; Tedford et al., 2009; among others). In Europe, the first occurrence of the modern wolf, with the subspecies *C. lupus lunellensis* (Bonifay, 1971), is reported at Lunel-Viel (France), chronologically referred to MIS 11–10 (0.4–0.35 Ma: Argant and Mallye, 2005; Mallye, 2007; Croitor et al., 2008; Boudadi-Maligne, 2010). Other subspecies of wolf have been described in France during the Pleistocene: *C. lupus santenaisensis* (Santenay site, MIS 6–5), *C. lupus mediterraneus* and *C. lupus maximus* (Jaurens Cave, MIS 3) (Bonifay, 1971; Argant, 1991; Brugal and Boudadi-Maligne, 2011; Boudadi-Maligne, 2012). In the Italian peninsula, the first record of the modern wolf is at La Polledrara di Cecanibbio (late Middle Pleistocene; Gliozzi et al., 1997; Petronio et al., 2011; Anzidei et al., 2012; Sardella et al., 2014). The morphology of *C. lupus* remains collected at La Polledrara di Cecanibbio is very similar to that of the modern wolf (Sardella et al., 2014). The modern wolf from the Apennine area is referred to the subspecies *C. lupus italicus* upon phenotypic (Altobello, 1921), morphometric (Nowak and Federoff, 2002; Nowak, 2003) and genetic features (Randi et al., 2000; Fabbri et al., 2007; Pilot et al.,

2010). No subspecies of *C. lupus* have been described in Italy through the Pleistocene.

In this paper, we investigated evolutionary models in the carnassial teeth of *C. lupus* from the Pleistocene of Southern Europe. Within canids, premolars and molars are used for slicing and for grinding, respectively (Ewer, 1973; Ungar, 2010). The upper carnassials, within all carnivores, are used only for slicing (Butler, 1946), whereas the lower carnassials play both functions in canids: the trigonid is used to slice and the talonid to grind (Ewer, 1973; Ungar, 2010). The ratio between trigonid and talonid is a valid indicator of the dietary habits (Ewer, 1973; Van Valkenburgh and Wayne, 1994; Ungar, 2010). The lower carnassial length can be used to estimate carnivore body size (Van Valkenburgh, 1990, 1991, 2007) due to its low variability and because tooth size is fixed upon eruption (Gingerich, 1974).

We focused on two questions: does exist an evolutionary trend in carnassial teeth of the wolf through the Pleistocene–Holocene? Does exist a relationship between climate change and carnassial teeth through time? We used linear measurements of European wolves to explore and better understand the evolutionary dynamics of the carnassial morphology during the Pleistocene using modern statistical tools.

## 2. Materials and methods

### 2.1. Materials

We collected 486 and 491 linear measurements (in mm) on the first lower molar and fourth upper premolar, respectively, i.e. the carnassial teeth (Fig. 1).

Data of extant and fossil *C. lupus* are from Argant (1991), Malez and Turk (1991), Ziegler (1996), Fladerer (1997), Fladerer and Einwögerer (1997), Pacher and Döppes (1997), Boudadi-Maligne (2010, 2012), Berté (2013), Berté and Pandolfi (2014) and Sardella et al. (2014). All of these authors strictly followed the morphometric methodology proposed by von den Driesch (1976). The measurements taken by Bouchud and Bouchud (1953), Bonifay (1971) probably followed a different approach. Details on the sample, localities and ages are reported in Table 1 and Figs. 1S and 2S.

### 2.2. Methods

We applied the model based functions available in “paleoTS” R package (Hunt, 2011) to test different evolutionary patterns summarized in Fig. 2.

This statistical tool provides the best-fitting evolutionary model of data (maximum likelihood) after testing four main phenotypic models of evolution: Unbiased Random walk (URW), General Random Walk (GRW), Stasis s.s. and Ornstein–Uhlenbeck (OU). URW indicates a fluctuation of the phenotype (population mean values) with no directionality, where the variance of the entire sample is larger than the individual populations variances (Fig. 2a). GRW model indicates a phenotypic fluctuation (population mean values) with a significant directionality; the trend can be typically directional (Fig. 2b) or related to a directional random walk (Fig. 2c).

Stasis s.s. indicates an evolutionary model wherein no trend appears in time and the variance of the entire sample is not larger than that of the individual populations (Fig. 2d). OU represents a random walk evolutionary model with a central tendency to an adaptive optimum of the phenotype (Fig. 2e).

However, a further case may occur when the total sample variance is larger than individual interval variance with no directionality (Fig. 2f).

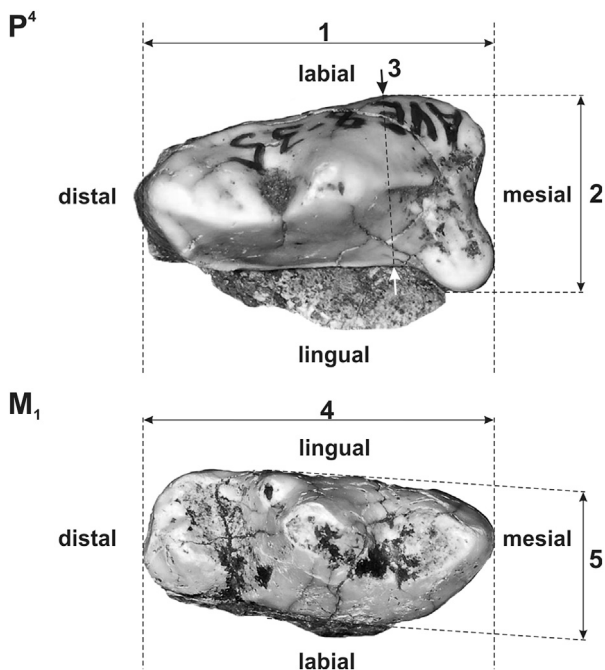


Fig. 1. Linear measurements calculated on the carnassials of *Canis lupus*. 1 = length of P<sup>4</sup>; 2 = maximum width of P<sup>4</sup>; 3 = width of P<sup>4</sup>; 4 = length of M<sub>1</sub> and 5 = width of M<sub>1</sub>.

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